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Origin context of trait data matters for predictions of community performance in a grassland biodiversity experiment

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Abstract. Plant functional traits may explain the positive relationship between species richness and ecosystem functioning, but species-level trait variation in response to growth conditions is often ignored in trait-based predictions of community performance. In a large grassland biodiversity experiment (Jena Experiment), we measured traits on plants grown as solitary individuals, in monocultures or in mixtures. We calculated two measures of community-level trait composition, i.e., community-weighted mean traits (CWM) and trait diversity (Rao's quadratic entropy; FD) based on different contexts in which traits were measured (trait origins). CWM and FD values of the different measurement origins were then compared regarding their power to predict community biomass production and biodiversity effects quantified with the additive partitioning method. Irrespective of trait origin, models combining CWM and FD values as predictors best explained community biomass and biodiversity effects. CWM values based on monoculture, mixture-mean or community-specific trait data were similarly powerful predictors, but predictions became worse when trait values originated from solitary-grown individuals. FD values based on monoculture traits were the best predictors of community biomass and net biodiversity effects, while FD values based on community-specific traits were the best predictors for complementarity and selection effects. Traits chosen as best CWM predictors were not strongly affected by trait origin but traits chosen as best FD predictors varied strongly dependent on trait origin and altered the predictability of community performance. We conclude that by adjusting their functional traits to species richness and even specific community compositions, plants can change community-level trait compositions, thereby also changing community biomass production and biodiversity effects. Incorporation of these plastic trait adjustments of plants in trait-based ecology can improve its predictive power in explaining biodiversity–ecosystem functioning relationships.

Key words: community-weighted mean traits; complementarity effects; experimental design; productivity; selection effects; trait diversity; trait plasticity; trait-based ecology.

Introduction

Approaches to use plant functional traits have steadily gained popularity in analyses of assembly processes and ecosystem functioning because they allow for the simultaneous evaluation of a large number of species (Webb et al. 2010). Functional traits are properties of organisms measured at the level of individuals, which influence the performance or fitness of organisms (Violle et al. 2007). The effects of functional traits on ecosystem processes are thought to be mediated by trait means and trait diversities in a community. Different metrics to quantify these and the choice of suitable indices has been intensively discussed (Schleuter et al. 2010, Pavoine and Bonsall 2011). Community-weighted mean traits (CWM), i.e., means of trait values typically weighted by species abundances in terms of aboveground plant biomass (Garnier et al. 2004), and trait diversity based on Rao's quadratic entropy (FD, Botta-Dukát 2005) are among the most popular indices (Ricotta and Moretti 2011). Trait-based analyses usually rest on the assumption that trait differences are much larger between species than within species (McGill et al. 2006). It is common practice to estimate trait-based indices using one single trait value per species, perhaps even taken from the literature or a database, thereby ignoring trait variation within a single species across or even within sites. Variation in trait values is caused by genetic differentiation or phenotypic plasticity in response to environmental conditions at large and at very fine scale and is known to be particularly large in plants with modular growth (McLellan et al. 1997).

Although several studies have emphasized that a species' trait expression varies with growth conditions (Albert et al. 2011), it is not clear how this variation is related to community-level trait composition and predictions of ecosystem functioning. Even if intraspecific trait variation in response to environmental variation is high, it is possible that trait-based rankings of species are conserved if trait differences

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among species are large or if different species shift their trait values in the same direction and to a similar extent (Garnier et al. 2001, Roscher et al. 2015). Effects of increased plant diversity on trait diversity dependent on the origin of trait data require a varying extent and direction of changes in trait values of the involved species in response to increased plant diversity to alter trait-trait distances among species in different origin contexts. Effects of increased plant diversity on CWMs, however, are largest when trait values of the involved species show changes in the same direction in response to increased plant diversity because otherwise the effects on different species could cancel each other out.

The positive species richness–productivity relationship observed in many biodiversity experiments has mainly been attributed to so-called complementarity and selection effects. They are usually calculated with an additive partitioning of the net biodiversity effect. The net biodiversity effect is itself defined as the difference between the value of an ecosystem function measured in mixture and the average value of that function across the monocultures of species making up the mixture (Loreau and Hector 2001). Positive complementarity effects should occur when communities consist of species representing a greater variety of traits and thereby are able to increase total resource use compared with communities comprising species with lower between-species trait variation. Positive selection effects are expected when a community contains species with particular traits, which have dominant effects on ecosystem properties (Fargione et al. 2007). More recently, biodiversity–productivity relationships in natural and experimental grasslands have also been explained with trait-based approaches (Díaz et al. 2007, Mokany et al. 2008, Schumacher and Roscher 2009, Flynn et al. 2011, Roscher et al. 2013). However, these approaches again mostly used single fixed trait values for each species taken from sources other than the actually studied plant communities. Recent work has highlighted the importance of recognizing within-species trait variation for estimations of trait diversity (Cianciaruso et al. 2009, de Bello et al. 2011, Roscher et al. 2015). No study has tested to what extent the origin context of trait measurements (here referred to as "trait origin") matters for explaining variation in ecosystem processes.

In the present study, we carried out such tests in a large grassland biodiversity experiment (Jena Experiment; Roscher et al. 2004) in which sown species richness ranged from monocultures to 2, 4, 8, 16 and 60 species. In addition, all species were also grown as solitary individuals. Previous studies in the Jena Experiment have shown that the expression of traits can vary with the changes in the diversity and composition of experimental plant communities (Thein et al. 2008, Gubsch et al. 2011*a*, Roscher et al. 2011*b*, Lipowsky et al. 2015). Here we show results of analyses based on four different species-specific trait datasets, all of them derived from measurements at the Jena Experiment field site, but accounting for different levels of plant–plant interactions: (1) without interactions (trait origin solitary-grown plants; Sol), (2) only intraspecific interactions (trait origin plants grown in monoculture: monoculture traits; Mono), (3) intra- plus average interspecific interactions (trait origin plants grown in mixtures, averaged across low- or high-diversity mixtures: mean-mixture traits; Mix) and (4) intra- plus community-specific interspecific interactions (trait origin plants grown in mixtures, not averaged across mixtures: community-specific traits; Com). First, we tested whether trait values differed between the four types of origin contexts (1–4) and how these influenced trait-based indices of community composition, i.e., CWM and FD values. Second, we explored the relationship between indices of different trait origin and community biomass production and biodiversity effects to evaluate (1) whether the origin of trait data influenced the predictability of community performance, (2) whether the relative importance of CWM and FD in predicting community performance depended on the origin of trait data, and (3) whether different traits were providing the best CWM and FD predictors of community performance for the different trait origins.

Methods

Experimental design

The Jena Experiment (Roscher et al. 2004) was established in May 2002 on former arable land. The site is located in the floodplain of the river Saale north to the city of Jena (Germany, 50°55′ N, 11°35′ E, 130 m a.s.l.). The region has a mean annual air temperature of 9.9°C, mean annual precipitation is 610 mm (1980–2010; Hoffmann et al. 2014). The soil is a Eutric Fluvisol developed from up to 2 m thick fluvial sediments that are almost free of stones. The biodiversity experiment was arranged in four blocks parallel to the river to account for a gradient in soil texture, ranging from loamy sand to silty clay with increasing distance from the riverside.

Central European mesophilic grasslands (Arrhenatherion type; Ellenberg 1988) were the base to choose a pool of 60 species for the Jena Experiment. Results of a cluster analysis based on a trait matrix with morphological, phenological and physiological characteristics derived from the literature served to classify these species into four functional groups: 16 grasses, 12 legumes, 20 tall herbs and 12 small herbs (Roscher et al. 2004). The design of the Jena Experiment is near-orthogonal, realizing all possible combinations of gradients in species richness (1, 2, 4, 8, and 16 species) and functional group number (1, 2, 3, and 4 functional groups). Each species-richness level had 16 replicates except for the 16-species mixtures with 14 replicates because two functional groups (legumes, small herbs) did not comprise enough species for mono-functional 16-species-mixtures. In addition, four plots with a mixture of all 60 species were set up resulting in a total of 82 plots of 20 × 20 m size. Species compositions for replicates of each species richness × functional group number combination (plots with 1–16 species) were determined by independent random draws with replacement from species of the respective functional groups. All species were also grown in replicated monocultures of 3.5 × 3.5 m size. An equal number of large-area plots per diversity level and small-area monocultures per functional group were randomly distributed among the four experimental blocks. All plots were established by sowing with a total density of 1,000 viable seeds per m^2 (adjusted for germination rates from laboratory trials) with even species proportions in the mixtures. To maintain the experimental plant communities, plants of species other than the ones originally sown to a plot were removed during two annual weeding campaigns (April, July). Plots

were mown twice per year (early June, September) as usual for extensively managed meadows in the region and did not receive any fertilizer.

Solitary plants of all species were grown with sufficient space between individuals to avoid competition. Four-month old seedlings pre-grown in the greenhouse from the same seed source as used for the experimental communities were transferred to the field site in June 2005 (for details see Roscher et al. 2011*a*). The seed bed was prepared after ploughing in November 2004 and raked several times in spring 2005 to remove emerging weed seedlings. Five (to ten) individuals per species were planted in the seed bed with planting distances between 0.8 and 2.5 m (dependent on the expected size of individual species). The open space between the solitary plant individuals was covered with black perforated foil (Aquafol, Hermann Meyer KG, Rellingen, Germany) to reduce evaporation and weed pressure. The growth of plant individuals was controlled regularly and if necessary foil was removed to open space around growing plant individuals.

Data collection

Aboveground biomass.—Aboveground plant material was harvested at estimated peak biomass shortly before mowing in late May 2006. Vegetation was clipped 3 cm above soil surface in subplots of 20 × 50 cm size. Four subplots were randomly placed in large plots, and two subplots were sampled in small monocultures. All samples were sorted to species sown into a particular community, separating unsown species and detached dead material. Plant material was dried to constant weight (70°C, 48 h) and weighed. For further details see Weigelt et al. (2010). Biomass of replicated samples per plot was averaged to calculate species and community biomass (g_{dw}/m^2).

Trait data.—Modules (=single shoots) were harvested to measure plant traits in one or two small-area monocultures per species and in all large-area mixtures (with exception of two replicates of the 60-species mixture) at the time of biomass harvest in late May 2006 except for six species. Data for these six species were collected in 2008 following the identical protocol. Five modules per species × plot combination were sampled when one life stage (vegetative, reproductive) dominated; three vegetative and three reproductive modules were taken when both stages were similarly present. Modules were selected along transects perpendicular to the plot margin (leaving out the outer 70 cm of the plots) at a minimum distance of 50 cm in large plots and 25 cm in small plots. Modules were cut off at ground level, put in sealed plastic bags in a cool box and transported to the laboratory. Similarly, five modules were also harvested from different solitary-grown plant individuals of each species. In the laboratory, stretched shoot length was measured before separating modules into leaves (being leaf blades in case of grasses, including petioles and rachis in case of herbs with compound leaves), stems (including leaf sheaths in case of grasses and secondary axes in case of herbs) and reproductive tissue (inflorescences, fruits). Leaf area was measured with a leaf area meter (LI-3100 Area Meter; Li-COR, Lincoln, Nebraska, USA) on one to five fully developed leaves per module (dependent on leaf size and number). All plant compartments were separately dried at 70°C (48 h) and weighed. Data from morphological measurements of single modules were averaged per life stage and species to calculate plot values. Measured leaf samples and bulk material of the remaining module compartments were pooled per species, life stage and plot, and ground to a fine powder for subsequent chemical analyses. Nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope ratios and elemental C and N concentrations were analyzed from leaf material (3 and 0.8 mg, respectively) with an isotope-ratio mass spectrometer ($Delta^{plus}XP$ and Delta C prototype IRMS respectively, Finnigan MAT, Bremen, Germany). Sample ratios of $^{15}N/^{14}N$ are expressed relative to the international standard of atmospheric N_2, and sample ratios of $^{13}C/^{12}C$ refer to the VPDB (Vienna Pee Dee Belemnite) international standard. Values are given in per mil relative to the standards. Approximately 20 mg of remaining bulk plant material was analyzed for carbon and nitrogen concentrations with an elemental analyzer (Vario EL Element Analyzer, Elementar, Hanau, Germany).

Functional traits derived from these measurements are summarized in Table 1. Six studied traits were associated with carbon gain and aboveground space filling. Specific leaf area (SLA) and carbon stable isotope ratios ($\delta^{13}C_{Leaf}$) are known to be related to photosynthetic capacity in unshaded conditions, but both are sensitive to changes in light and nitrogen availability (Dawson et al. 2002, Cornelissen et al. 2003). Shoot length (L_{Shoot}), stem mass fraction (SMF), shoot carbon concentrations (C_{Shoot}) and mass : height ratios (MHR) reflect competitive vigor in light acquisition and space filling as well as the investment in supporting tissue to achieve structural stability (Gubsch et al. 2011*a*). Three traits were related to nitrogen acquisition and use, i.e., shoot nitrogen concentrations (N_{Shoot}) and leaf nitrogen concentrations (N_{Leaf}) as well as nitrogen isotope ratios ($\delta^{15}N_{Leaf}$). The natural isotope ratios of $\delta^{15}N_{Leaf}$ are the net result of numerous processes such as the presence of various N sources with distinct isotopic signatures, mycorrhizal associations, temporal and spatial variation in N availability and the dependency on symbiotic N_2 fixation in case of legumes (Högberg 1997, Dawson et al. 2002).

Data analysis

The additive partitioning method (Loreau and Hector 2001) was applied to quantify biodiversity effects on mixture biomass production. According to this method, the net biodiversity effect (NE) is the difference between the observed biomass in a mixture and the expected biomass based on the average of monoculture biomass of the component species. The NE is partitioned into two additive components, the complementarity effect (CE) and the selection effect (SE)

$$\mathrm{NE} = \mathrm{CE} + \mathrm{SE} = S\overline{\Delta \mathrm{RY}}\ \overline{M} + S\,\mathrm{cov}(\Delta \mathrm{RY}, M) \quad (1)$$

where S is the number of species in the mixture, ΔRY is the difference between the observed relative yield and the expected relative yield (i.e., its sown proportions) of a species in the mixture, and M is the monoculture biomass of that species. Averaged biomass data of the two small monocultures per species were used for all calculations.

TABLE 1. Overview of functional traits derived from trait measurements.

Trait	Abbreviation	Function	Unit	Description
Shoot length	L_{Shoot}	Light acquisition	cm	Stretched shoot length
Mass to height ratio	MHR	Light acquisition	mg_{shoot}/cm_{shoot}	Shoot dry mass per unit length
Stem mass fraction	SMF	Light acquisition	mg_{stem}/mg_{shoot}	Stem dry mass per shoot dry mass
Specific leaf area	SLA	Light acquisition	mm^2_{leaf}/mg_{leaf}	Leaf area per leaf dry mass
Shoot carbon concentration	C_{Shoot}	Light acquisition	$mg\ C/g_{shoot}$	Carbon mass per shoot dry mass
Leaf $\delta^{13}C$	$\delta^{13}C_{Leaf}$	Light acquisition	‰	^{13}C isotopic signature of leaves
Shoot nitrogen concentration	N_{Shoot}	Nitrogen acquisition	$mg\ N/g_{shoot}$	Nitrogen mass per shoot dry mass
Leaf nitrogen concentration	N_{Leaf}	Nitrogen acquisition	$mg\ N/g_{leaf}$	Nitrogen mass per leaf dry mass
Leaf $\delta^{15}N$	$\delta^{15}N_{Leaf}$	Nitrogen acquisition	‰	^{15}N isotopic signature of leaves

Traits (Table 1) and species biomass proportions were used to calculate community-weighted mean traits (CWMs) according to the equation

$$\mathrm{CWM} = \sum_{i=1}^{S} p_i t_i \tag{2}$$

where S is the number of species in the community, p_i are the species biomass proportions, and t_i are species-specific trait values (Garnier et al. 2004).

Trait diversity (FD) was computed using Rao's quadratic entropy (Rao 1982)

$$\mathrm{FD} = \sum_{i=1}^{S} \sum_{j=1}^{S} p_i p_j d_{ij} \tag{3}$$

where S is the number of species in the community, p_i and p_j are the biomass proportions of species i and j, and d_{ij} is the trait distance between species i and j in the community. To assess the impact of trait variation in different environments (trait origin) on both measures, all calculations were based on (1) trait values measured on the solitary plants (Sol), (2) trait values measured in species monocultures (Mono), (3) trait values measured in mixtures as means across low- or high-diversity mixtures (Mix), and (4) trait values measured in mixtures as community-specific trait values (Com). Community-specific trait values are affected by the diversity and the composition of the studied communities, while mixture-mean trait values (Mix) across different compositions better account for biodiversity effects on trait expression. Since mixture compositions were randomly created in the Jena Experiment, individual species do not necessarily occur several times per sown species-richness level (Appendix S1: Table S1 for species occurrences per diversity level). To better differentiate between mixture-mean trait values (Mix) and community-specific trait values (Com), we therefore averaged traits for low-diversity (2–8 species) and high-diversity (16 and 60 species) mixtures in our analysis of mixture-mean traits. In cases where trait values for vegetative and reproductive modules were available, it was assumed for weighting that both stages contributed equal proportions to that species' biomass proportion in a community (see Appendix S1: Table S2 for mixture compositions). For three grass species (*Bromus hordeaceus* L., *Cynosurus cristatus* L., *Holcus lanatus* L.) tissue chemical traits were not available from the solitary-grown plants; these values were replaced with the respective values from the monocultures. Monoculture trait values were not available for two species (*Cardamine pratensis* L., *Luzula campestris* (L.) (Dc.); these values were substituted by trait values from a low-diversity mixture (4 species). In 21 out of 575 cases species occurred in the biomass samples of the mixtures, but community-specific trait data were not available. In these cases, community-specific trait values were replaced by mean values across all mixtures in which these species could be measured. If necessary, trait data were log-transformed for calculations of FD based on a Euclidian distance matrix, while no transformations were applied in calculations of CWMs. All indices were calculated using the library *FD* (Laliberté and Shipley 2010) of the statistical software R (version 3.0.2, R Development Core Team, http://www.R-project.org).

In a first analysis step, mixed-effects models using the lmer function in the R library lme4 (Bates et al. 2012) were applied to assess whether (1) intraspecific trait variation affected CWMs and FDs, and (2) effects of trait variation increase with increasing plant diversity. Modeling was initiated from a constant null model with block and plot (nested in block) as random-effects terms. The null model was extended stepwise by entering terms for trait data of different origin (Origin; with four factor levels: Sol = traits of solitary plants; Mono = monoculture traits; Mix = mixture-mean traits; Com = community-specific traits), sown species richness (SR; log-linear), functional group number (FG; linear) and the interaction of Origin with plant diversity (SR × Origin, FG × Origin). The maximum likelihood method and likelihood ratio tests were applied to test for model improvement and the statistical significance of the fixed effects. Differences between measures based on different trait origin (Sol, Mono, Mix, Com) were identified with Tukey's HSD test applying the glht function in the package multcomp (Hothorn et al. 2008) in models fitted with the restricted maximum likelihood method (REML).

In a second step, mixed-effects models were used to identify the best predictor combination for variation in community biomass and biodiversity effects (NE, CE, SE) using CWMs and FDs of the different traits as explanatory terms, i.e., predictor variables. Block was treated as random-effects term in a global model comprising all candidate predictors. An automated model selection procedure (dredge function in the R library MuMIn; Bartón 2016) was applied to generate the best five models with subsets of the terms from the global model based on the AIC_c (second-order Akaike information criterion).

Coefficients of determination (R^2 measure of goodness of fit) were calculated for the best five models based on likelihood ratio test statistics (Magee 1990) comparing the log-likelihood of the final models with the log-likelihood of the null model (intercept-only model). Analyses were performed separately using either CWMs or FDs of traits alone or CWMs and FDs in combination as predictor variables, and were repeated with calculations based on different sets of trait data. In the main text we present the best model, while the best five models are shown in the Supplementary Material (Appendix S1: Tables S4–S7). Apart from differences in goodness of model fit dependent on trait origin, it is also possible that trait origin determines the identity of CWMs or FDs included in the best statistical models. To test this possibility, we used the best predictor combination identified in analysis with community-specific trait data (Com), fitted the same model with traits of different origin (Sol, Mono, Mix) and compared goodness of fit of the different models. We confined these analyses to models with community-specific trait values as a baseline because we were particularly interested to explore whether community-specific trait values would be superior in predicting community performance. However, in this way our test is less likely to find that predictor combinations based on other origins in some contexts work better than those based on community-specific traits.

Results

Differences between trait values measured in mixtures, monocultures or on solitary plants

Species means of trait values measured in mixtures were more strongly correlated with trait values measured in the monocultures ($0.584 \leq r_s \leq 0.960$) than with trait values measured on solitary plants ($0.418 \leq r_s \leq 0.827$; compare Appendix S1: Figs. S1, S2). Solitary plants had the largest trait values, with the exception of SLA (largest values in mixtures), SMF and C_{Shoot} (both not significantly different between solitary plants and monocultures or mixtures; Appendix S1: Figs. S1, S3). Species means of L_{Shoot}, SMF, SLA, C_{Shoot} and N_{Leaf} were larger in mixtures than in monocultures, while species means of MHR, leaf $\delta^{13}C$ and leaf $\delta^{15}N$ were larger in monocultures than in mixtures (paired t test; Appendix S1: Fig. S2). Species means of N_{Shoot} did not differ significantly between monocultures and mixtures.

Community-weighted mean traits (CWMs)

Trait variation in response to different growth conditions had significant effects on CWMs for all studied traits (Fig. 1, Table 2). In particular, CWMs originating from measurements on solitary plants differed significantly from CWMs originating from measurements on plants growing in monocultures or mixtures (Tukey's HSD: $P < 0.001$), with the exception of CWM-C_{Shoot}, which was not different when traits were measured in the mixtures. Nevertheless, CWMs based on community-specific traits were highly correlated with CWMs based on trait data of different origins in all studied traits (Appendix S1: Fig. S4).

CWM-$\delta^{13}C_{Leaf}$ (Mono > Com > Mix) also varied between the three trait origins in monocultures or mixtures (Fig. 1f). The same was the case for CWMs for other leaf traits (CWM-SLA, CWM-N_{Leaf}, CWM-$\delta^{15}N_{Leaf}$), but here the two mixture trait origins gave similar results (i.e., Mix ≈ Com). Monoculture-based CWM-SLA and CWM-N_{Leaf} were smaller and CWM-$\delta^{15}N_{Leaf}$ was larger than CMWs based on mixture traits (Fig. 1d, h, i). CWMs for whole-shoot traits did not differ between monocultures and mixtures.

CWMs for SMF increased and CWMs for $\delta^{13}C_{Leaf}$ decreased with increasing species richness independently of trait origin (Fig. 1c, f), while species richness effects on CWMs for L_{Shoot} (increase) and $\delta^{15}N_{Leaf}$ (decrease) depended on trait origin (Fig. 1a, i; Table 2). For both variables, CWMs were more strongly related to species richness effects when calculated with community-specific or mixture-mean values than with monoculture values (Appendix S1: Table S3). When values from solitary plants were used for the calculations, CWM-L_{Shoot} showed a weak association with species richness (Fig. 1a); and CWM-$\delta^{15}N_{Leaf}$ did not show any relation to species richness (Fig. 1i; Appendix S1: Table S3).

Trait diversity (FD)

The origin of the plants on which traits were measured also affected FD values for all traits (Fig. 2, Table 2). Correlations between FDs based on community-specific traits and FDs based on traits of solitary-grown plants were generally weaker (Appendix S1: Fig. S5). Correlations were strongly significant for all traits when FDs based on community-specific traits were compared with FDs based on monoculture or mixture-mean traits. FDs for L_{Shoot}, SMF, SLA, N_{Shoot}, N_{Leaf} and $\delta^{15}N_{Leaf}$ were underestimated with trait values from solitary-grown plants compared to FDs based on traits measured in monocultures or mixtures (Appendix S1: Table S3). In contrast, FD-C_{Shoot} based on data from solitary-grown plants was larger than FDs from monocultures, but not different from FDs based on mixture-mean or community-specific data. FD-SLA from solitary-grown plants was smaller than FDs from mixture-mean or community-specific data, but did not differ from FD-SLA based on monoculture data. FDs mostly did not vary between the three trait origins in monocultures or mixtures. Indices based on monoculture data underestimated FD based on community-specific data for SLA (Fig. 2d). FD-$\delta^{13}C_{Leaf}$ was greater when community-specific data instead of mixture-mean data were used (Fig. 2f).

Trait diversity increased with increasing species richness in all studied traits as would be expected. An increasing number of functional groups had additional positive effects on FD in traits related to nitrogen-acquisition (N_{Shoot}, N_{Leaf}, $\delta^{15}N_{Leaf}$) and whole-shoot traits (L_{Shoot}, SMF, C_{Shoot}; Table 2). The closer the FD values for SLA and $\delta^{15}N_{Leaf}$ were measured under the specific conditions under which the plants grew, the stronger they were related to species richness, i.e., positive effects of these terms generally decreased in the order community-specific > mixture-mean > monoculture > solitary-plant trait origin, while the opposite was the case for $\delta^{13}C_{Leaf}$ (see significant interaction

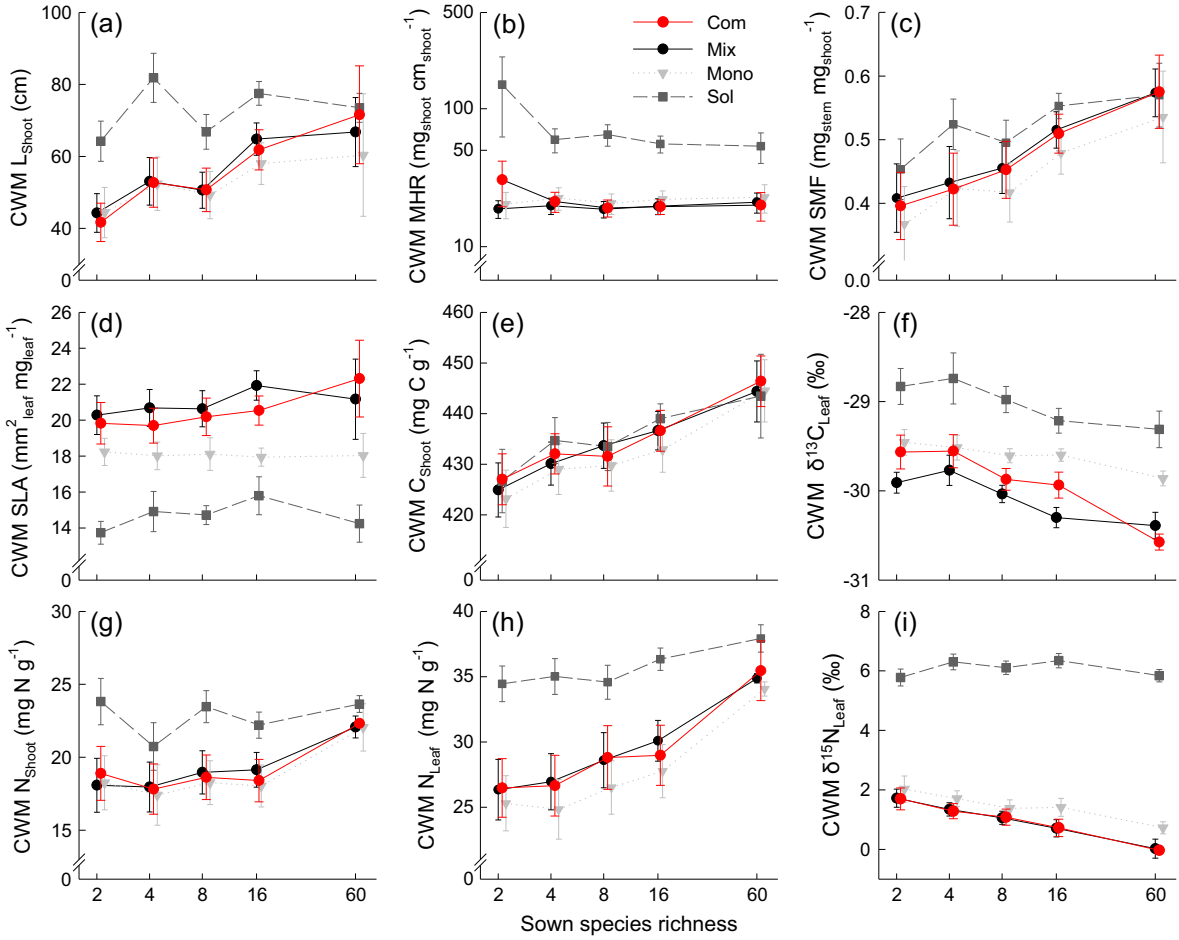

FIG. 1. Community-weighted means (CWM) for (a) shoot length, (b) mass to height ratio, (c) stem mass fraction, (d) specific leaf area, (e) shoot carbon concentration, (f) leaf $\delta^{13}C$, (g) shoot nitrogen concentration, (h) leaf nitrogen concentration, and (i) leaf $\delta^{15}N$ based on traits measured on solitary-grown plants (Sol), in monocultures (Mono), in the mixtures as mean across communities of low or high species richness (Mix) and as community-specific values (Com). Shown are means (±1 SE) per sown species-richness level.

Origin × SR for FD-SLA, FD-$\delta^{15}N_{Leaf}$ and FD-$\delta^{13}C_{Leaf}$ in Table 2 and estimated coefficients in Appendix S1: Table S3). In contrast, the significant interactions Origin × FG for FD-SMF, FD-N_{Shoot} und FD-N_{Leaf} were mostly due to smaller positive effects of functional group numbers when FDs were based on measurements from solitary-grown plants (Appendix S1: Table S3).

Trait-based predictions of biomass production

Irrespective of trait origin, models based on CWMs alone (M_{CWM}) better predicted biomass production than models based on FDs alone (M_{FD}; larger R^2; Fig. 3a; Appendix S1: Table S4). In M_{CWM}, goodness of model fit was lowest when the traits were measured on solitary-grown plants ($M_{CWM\text{-}Sol}$), but did not differ greatly when traits were measured under monoculture or mixture growth conditions (Fig. 3a). In models based on community-specific trait values ($M_{CWM\text{-}Com}$), high CWMs for L_{Shoot}, MHR, C_{Shoot}, N_{Shoot} and low CWM-$\delta^{15}N_{Leaf}$ were the most important predictors for high community biomass production. Similar trait combinations were chosen in models based on mixture-mean or monoculture traits, but did not include CWM-$\delta^{15}N_{Leaf}$ in models based on monoculture trait values ($M_{CWM\text{-}Mono}$) and CWM-C_{Shoot} in models based on mixture-mean trait values ($M_{CWM\text{-}Mix}$). In contrast, the traits incorporated in the best $M_{CWM\text{-}Sol}$ did not include positive effects of CWM-L_{Shoot}, and CWM-N_{Leaf} replaced CWM-N_{Shoot}.

Selecting best models based on FD alone largely depended on trait origin (M_{FD}), but this was not the case for models based on both predictor groups (CWM, FD). Again, model fits were poorest when traits had been measured on solitary plants. However, M_{FD} fits based on community-specific traits were poorer than when traits were measured in monocultures or averaged across mixtures (Fig. 3a; Appendix S1: Table S4). While four traits were chosen for the $M_{FD\text{-}Mono}$ and $M_{FD\text{-}Mix}$ (positive effects of FD-L_{Shoot}, FD-$\delta^{15}N_{Leaf}$, negative effects of FD-SMF, FD-$\delta^{13}C_{Leaf}$), the best $M_{FD\text{-}Com}$ comprised FD-SMF (negative effects), FD-SLA and FD-$\delta^{15}N_{Leaf}$ (both positive effects). The best $M_{FD\text{-}Sol}$ was based on the choice of four traits, which were in part common to the models based on monoculture or mixture-mean traits (FD-SMF, FD-$\delta^{13}C_{Leaf}$), but additionally included FD-MHR (negative effects) and FD-C_{Shoot} (positive effects; Table 3). Generally, the fit of models including both CWMs and FDs as predictors were better than M_{CWM}. Models

TABLE 2. Summary of mixed-effects model analyses of community-weighted mean traits (CWM) and trait diversity (FD) comparing indices based on trait data of different origin context.

Source of variation	L_{Shoot}		MHR		SMF		SLA		C_{Shoot}		$\delta^{13}C_{Leaf}$		N_{Shoot}		N_{Leaf}		$\delta^{15}N_{Leaf}$	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Community-weighted mean traits (CWM)																		
Origin	127.40	<0.001	215.53	<0.001	58.25	<0.001	177.09	<0.001	14.14	0.003	162.75	<0.001	134.57	<0.001	168.27	<0.001	424.23	<0.001
SR	3.94	0.047	0.11	0.742	3.99	0.046	0.88	0.349	3.72	0.054	6.12	0.013	0.17	0.676	2.56	0.109	4.49	0.034
FG	0.39	0.533	0.04	0.833	0.37	0.545	0.33	0.565	1.69	0.193	0.71	0.399	0.24	0.622	0.92	0.338	2.52	0.112
SR × Origin	8.73	0.033	2.67	0.446	2.34	0.504	3.09	0.378	0.60	0.897	3.75	0.289	4.95	0.175	3.95	0.267	31.29	<0.001
FG × Origin	2.27	0.518	2.12	0.549	0.87	0.834	1.22	0.749	2.25	0.523	1.89	0.596	2.63	0.452	0.09	0.994	6.44	0.092
Trait diversity (FD)																		
Origin	36.55	<0.001	8.56	0.036	82.52	<0.001	39.80	<0.001	11.31	0.010	9.56	0.023	65.86	<0.001	69.36	<0.001	77.60	<0.001
SR	16.40	<0.001	11.88	0.001	5.15	0.023	20.62	<0.001	15.41	<0.001	33.75	<0.001	11.44	0.001	21.27	<0.001	28.20	<0.001
FG	10.99	0.001	3.50	0.061	7.05	0.008	0.05	0.816	9.25	0.002	3.32	0.069	16.49	<0.001	9.19	0.002	20.02	<0.001
SR × Origin	4.26	0.234	1.00	0.801	1.29	0.732	11.93	0.008	2.25	0.522	7.89	0.048	3.39	0.336	4.08	0.252	8.08	0.044
FG × Origin	5.49	0.139	1.51	0.681	12.11	0.007	1.12	0.773	4.36	0.225	5.36	0.147	17.14	0.001	27.64	<0.001	3.89	0.274

Notes: Models were fitted by adding fixed effects stepwise. Listed are the results of likelihood ratio tests (χ^2) that were applied to assess model improvement and the statistical significance of the fixed effects (P values). SR, species richness; FG, functional group number; Origin, origin of trait data (with four factor levels). For abbreviations of trait variables please refer to Table 1.

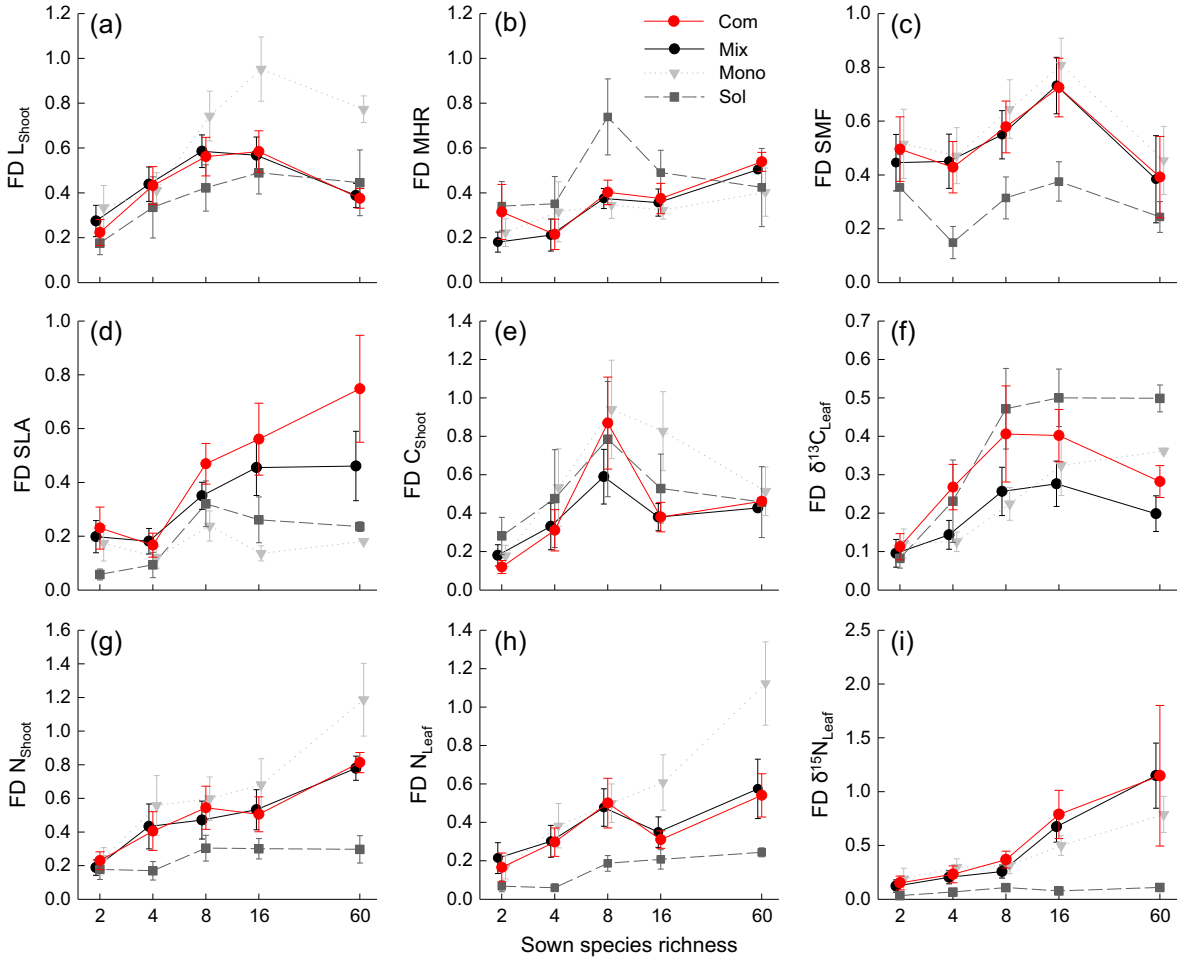

FIG. 2. Trait diversity (FD) for (a) shoot length, (b) mass to height ratio, (c) stem mass fraction, (d) specific leaf area, (e) shoot carbon concentration, (f) leaf $\delta^{13}C$, (g) shoot nitrogen concentration, (h) leaf nitrogen concentration, and (i) leaf $\delta^{15}N$ based on traits measured on solitary-grown plants (Sol), in monocultures (Mono), in the mixtures as mean across communities of low and high species richness (Mix) and as community-specific values (Com). Shown are means (±1 SE) per sown species-richness level.

based on traits measured in monoculture or the mean across mixtures were slightly better in predicting community biomass production than models based on community-specific traits (Fig. 3a). Additional analysis using the best predictor combination identified in analysis with community-specific trait data in models with different trait origin showed that model fit remained similar with monoculture traits, but was lower with mixture-mean traits (Fig. 3b).

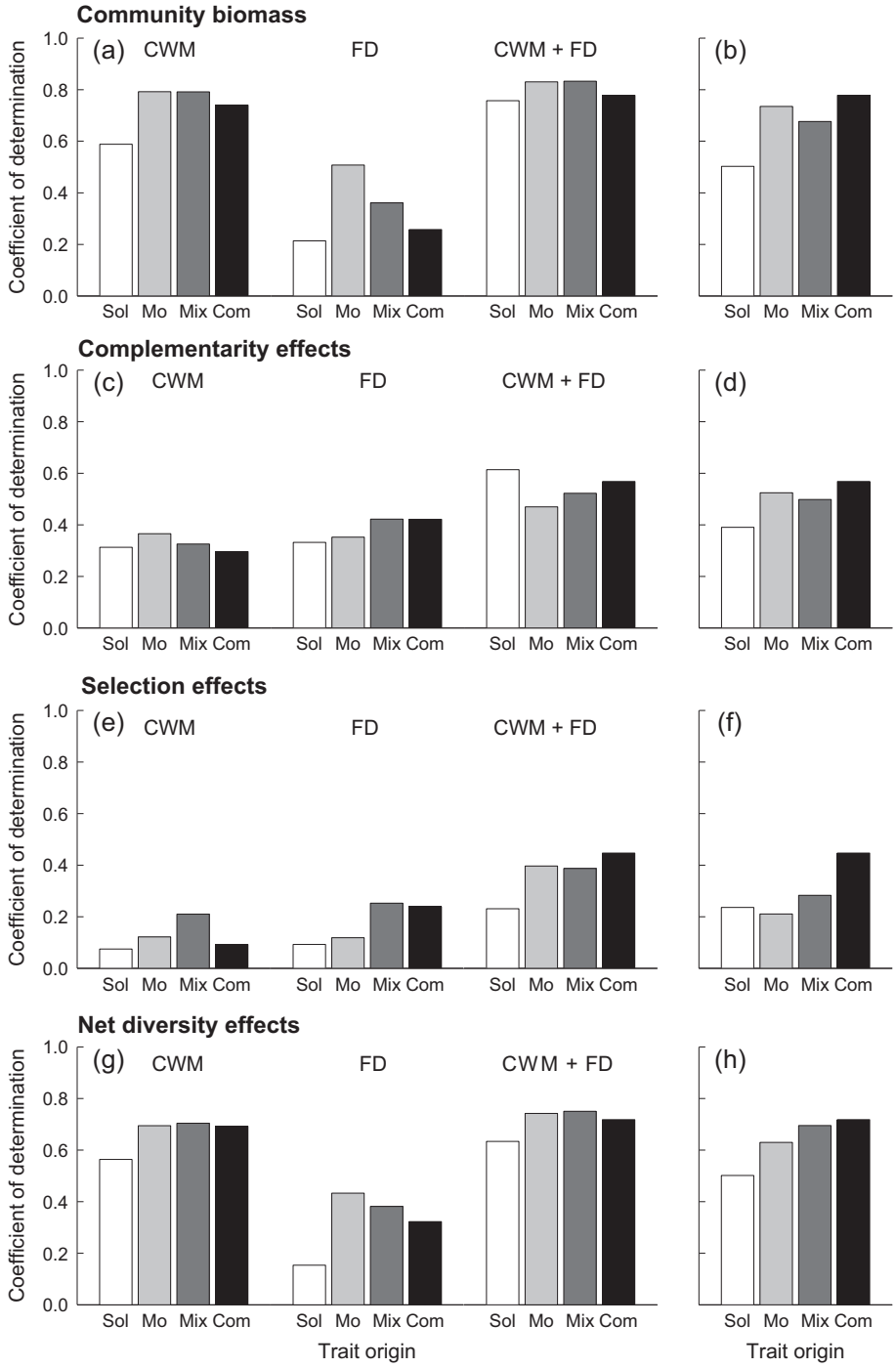

FIG. 3. Coefficients of determination for the best statistical models (a, c, e, h) based on traits measured on solitary-grown plants (Sol), in monocultures (Mo), in mixtures as mean across communities of low or high species richness (Mix) and as community-specific values (Com), and a model with the variable combination of the best statistical model based on community-specific traits using traits of different origin (b, d, f, h) for community biomass (a, b), complementarity effects (c, d), selection effects (e, f), and net biodiversity effects (g, h). The choice of best models was based on the AIC criterion (Table 3). For community-specific traits, models presented in the right-hand panels (b, d, f, h) are the same as in the left-hand panels (a, c, e, h) for predictions with CWM and FD in combination.

Trait-based predictions of complementarity, selection and net biodiversity effects

The origin of trait data had small effects on model fits in predicting complementarity effects (CE; Appendix S1: Table S5; Fig. 3c). While model fits were similar for models based on CWM (M_{CWM}) or FD (M_{FD}) alone, the combination of both (CWM and FD) slightly improved model fits irrespective of trait origin. CWM-N_{Shoot} (positive effects) was the single predictor most consistently chosen for M_{CWM} with the lowest AIC_c, with the exception for modelling with trait data from solitary-grown plants. For community-

TABLE 3. Summary of best statistical models for community biomass, complementarity effects, selection effects and net biodiversity effects based on different groups of predictor variables in models using different trait origins: model (A) with community-weighted mean traits (CMW) as predictors, model (B) with trait diversity (FD) as predictors and model (C) with both predictor groups.

			Community-weighted means (CWM)									Trait diversity (FD)									
	Origin	Intercept	L_{Shoot}	MHR	SMF	SLA	C_{Shoot}	$\delta^{13}C$	N_{Shoot}	N_{Leaf}	$\delta^{15}N$	L_{Shoot}	MHR	SMF	SLA	C_{Shoot}	$\delta^{13}C$	N_{Shoot}	N_{Leaf}	$\delta^{15}N$	AIC_c
Community biomass																					
A	Sol	−4.374		0.256			0.018			0.059	−0.165										102.1
A	Mono	−8.611	0.529	0.366			0.016	1.345	0.736												60.9
A	Mix	2.593	0.017	0.209				1.031	0.045		−0.309										61.2
A	Com	−0.499	0.013	0.202			0.011		0.025		−0.151										75.2
B	Sol	5.853											−0.296	−0.153		0.260	0.189				143.5
B	Mono	5.888										0.703		−0.860			−0.183			0.500	113.5
B	Mix	5.830										0.756		−0.693			−0.164			0.379	130.2
B	Com	6.071												−0.366	0.281					0.164	137.2
C	Sol	−1.278	0.008	0.148			0.015			0.052	−0.299		−0.176		0.165	0.195					79.3
C	Mono	−5.422	0.564	0.288			0.010	1.944	0.485		−0.509								0.128		53.5
C	Mix	2.323	0.017	0.286				1.150	0.043		−0.293						−0.089	0.169			52.5
C	Com	−1.151	0.015				0.012		0.063					0.241			0.220		−0.134		67.9
Complementarity effects																					
A	Sol	−0.535	−0.019	0.449			0.014	−0.674													167.3
A	Mono	1.087							1.574												154.9
A	Mix	3.248		0.299					0.078												161.1
A	Com	4.109		0.281					0.045		−0.181										163.6
B	Sol	5.876														0.293	0.297		−0.257		163.0
B	Mono	6.172																	0.439		156.2
B	Mix	6.488														0.269				0.336	151.2
B	Com	6.296										−0.413	0.382							0.274	153.8
C	Sol	9.654			−1.951			−1.032			−0.291	0.172			0.192	0.165	0.176		−0.257		141.4
C	Mono	−3.672	−0.532	0.520						2.700	1.086			0.543	0.156						139.5
C	Mix	3.907		0.488					0.048									0.207	0.247		144.0
C	Com	3.694		0.460					0.051			−0.663		0.447				0.409			140.2
Selection effects																					
A	Sol	−485.1			843.3																966.5
A	Mono	2797.0							−579.7		−815.6										965.6
A	Mix	2196.0	10.2							−769.1	−222.5										961.3
A	Com	−356.1	5.738																		965.3
B	Sol	−242.7												−92.2							965.3
B	Mono	−119.3										228.4		−368.1							965.8
B	Mix	−170.3										463.8	254.3	−448.2					−204.6		960.3
B	Com	−162.8										475.2		−457.1					−96.1		958.8
C	Sol	73.3	8.4								−108.7	−128.8							114.6		962.1
C	Mono	−5300.3				−41.1	15.4	1277.2		−916.3		417.4	182.9	−598.3	−156.4						957.6
C	Mix	1658.9	7.8							−611.1	−268.4		181.5			−131.1			−146.6		952.9
C	Com	−3204.4	9.9	−253.0	−1496.4		9.2					451.7		−440.7			145.4		−190.5		952.0
Net biodiversity effects																					
A	Sol	0.987		0.274			0.012	−0.626			−0.181										76.8
A	Mono	−5.502		0.392			0.015	1.218		0.601											54.0
A	Mix	0.447	0.014		−1.489		0.012	0.520			−0.316										54.6
A	Com	0.332	0.015		−1.902		0.009			0.525	−0.153										56.9
B	Sol	6.339											−0.296			0.135				0.184	116.7
B	Mono	6.230										0.440		−0.649						0.372	91.0
B	Mix	6.046												−0.289			−0.137			0.329	96.6
B	Com	6.208												−0.354	0.234					0.151	102.4
C	Sol	0.408		0.220			0.014	−0.594			−0.175					0.118					68.2
C	Mono	−5.766		0.307		−0.046	0.013	2.128		0.792								0.148			48.5
C	Mix	4.496	0.017		−1.337			0.821	0.027		−0.337						−0.118	0.145			49.1
C	Com	0.722	0.017		−1.878		0.011		0.025		−0.098						0.123				54.2

Notes: Trait origins: solitary-grown plants (Sol), monocultures (Mono), mixtures, where values were means across low- and high-diversity mixtures (Mix), community-specific values (Com). Abbreviations of variable names are explained in Table 1.

specific trait data, the best model additionally comprised CWM-MHR (positive effects) and CWM-$\delta^{15}N_{Leaf}$ (negative effects). CWM-MHR was also incorporated in the best model with mixture-mean traits.

Traits incorporated in M_{FD} were more variable dependent on their origin (Table 3), and this was also the case for models combing CWM and FD as predictors. The model based on community-specific trait values comprised CWM-MHR, CWM-N_{Shoot} (both positive effects) and FD-L_{Shoot} (negative effects), FD-SMF and FD-N_{Shoot} (both positive effects). Using the same predictor combination in models with different trait origin showed that the goodness of fit was similar with monoculture or mixture-mean traits, while model fits were poorer with traits from solitary-grown plants (Fig. 3d).

Separate M_{CWM} and M_{FD} led to similar model fits in explaining selection effects (SE) irrespective of trait origin with the exception of community-specific trait data, where M_{FD} alone had a better model fit than M_{CWM} alone (Table 3). In M_{CWM}, the fit was best with mixture-mean traits. While CWM-SMF (positive effects) was the best predictor of SE in M_{CWM} when traits were measured on solitary plants, CWM-N_{Shoot} and CWM-$\delta^{15}N_{Leaf}$ (both negative effects) were chosen as best-fit models when monoculture traits were used. The best models based on mixture-mean or community-specific trait values included CWM-L_{Shoot} (positive effects), and the mixture-mean model additionally comprised CWM-N_{Leaf} and CWM-$\delta^{15}N_{Leaf}$ (both negative effects). Irrespective of trait origin, the separate M_{FD} nearly always comprised FD-SMF and FD-L_{Shoot} (both negative effects) in models with the best fit. In addition, FD-N_{Leaf} (negative effects) was incorporated in models with mixture-mean and community-specific traits, and the best mixture-mean model additionally comprised FD-MHR (positive effect). Again, irrespective of the origin of trait data, selection effects were best explained when both CWM and FD were considered (Table 3). The best model fit was achieved with community-specific trait data and included eight predictor variables. Four of these were based on CWM: L_{Shoot}, C_{Shoot} (positive effects) and SMF, MHR (negative effects). The four included predictors based on FD were related to shoot architecture (L_{Shoot} = positive effects, SMF = negative effects) or leaf physiology (N_{Leaf} = negative effects, CWM-$\delta^{13}C_{Leaf}$ = positive effects). Model fits were poorer and other trait combinations were chosen when the combined CWM-FD models were based on other trait origins (Appendix S1: Table S6; Fig. 3e). When the predictor combination from the best model with community-specific trait data was used in modelling with different trait origins model fits also decreased (Fig. 3f).

The models best explaining net biodiversity effects (NE) gave a similar fit for monoculture, mixture-mean and community-specific traits in separate M_{CWM}. Model fit was slightly better for models with monoculture or mixture-mean trait data than for community-specific trait data in separate M_{FD} or models with CWM and FD (Appendix S1: Table S7; Fig. 3g). Models based on traits of solitary plants had a slightly poorer fits in M_{CWM} and models with CWM and FD, but model fits were considerably poorer in separate M_{FD}. Separate M_{CWM} explained variation in NE better than separate M_{FD}, but the combination of both gave the best model fit (Fig. 3g). Dependent on trait origin, the best models comprised different sets of predictor variables. Irrespective of whether traits were mixture-means or community-specific values, the best models included CWM of whole-shoot traits (L_{Shoot} = positive effects, SMF = negative effects) and of traits related to nitrogen acquisition (N_{Shoot} = positive effects, $\delta^{15}N_{Leaf}$ = negative effects), but were more variable in other incorporated traits (Table 3). Again, the predictor combination from the best model with community-specific traits resulted in poorer model fits if trait origin was changed (Fig. 3h).

Discussion

Context-specificity of trait expression and indices of community trait composition

In previous analyses of trait data from the Jena Experiment we have shown that different species within the functional groups of grasses (Gubsch et al. 2011*a*), legumes (Roscher et al. 2011*b*) and herbs (Lipowsky et al. 2015) vary widely in the extent and to some degree in the direction of trait variation along the experimental plant diversity gradient. Our present analysis showed that trait values of different origin context are often significantly correlated and that the direction of trait variation in response to growth conditions was similar across species (Appendix S1: Figs. S1–S3). It is not surprising—but relevant for prediction—that trait values and the calculated values of CWMs and FDs based on measurements of solitary plants with unlimited access to resources were most different from values of CWMs and FDs based on measurements made in monocultures or mixtures (Figs. 1, 2; Appendix S1: Figs. S4, S5). The higher trait values of individual species and CWM in L_{Shoot}, MHR and SMF based on the values of solitary plants (Fig. 1a–c; Appendix S1: Fig. S1a–c) showed that species used the unlimited space for spatial expansion and consequently also invested more biomass in supporting tissue. Lower values of SLA (Fig. 1d; Appendix S1: Fig. S1d) and higher values of $\delta^{13}C_{Leaf}$ (Fig. 1f; Appendix S1: Fig. S1f) indicated that the species growing under full-light conditions as solitary plants formed sun leaves with a greater photosynthetic capacity (Farquhar et al. 1989). Conversely, species-level values and CWM in shoot architectural traits recorded in the monocultures and mixtures revealed that plants were limited in their spatial expansion (low CWM-MHR) and also invested in height growth. However, higher CWM-SLA and lower CWM-$\delta^{13}C_{Leaf}$ suggested that not all species had access to full light and tolerated canopy shade, with the formation of shade leaves with larger SLA and a lower photosynthetic capacity (as also confirmed by differences in species-level values, Appendix S1: Fig. S1). This also applies to monocultures, where larger individuals likely shaded smaller ones. However, CWM-SLA based on monoculture SLA was smaller than CWM-SLA with mean-mixture or community-specific values (Fig. 1d). The opposite patterns were observed for CWM-$\delta^{13}C_{Leaf}$ (Fig. 1f) suggesting that in more diverse communities more species grew in the canopy shade and responded sensitively to their actual growth environment (Appendix S1: Table S3).

FDs in shoot-architectural traits and SLA based on the solitary plants were remarkably smaller than FDs based on these traits recorded in monocultures or mixtures. Thus, plants interacting with neighbours diverged in their light-acquisition characteristics, thereby increasing the options for a more complete use of light resources in the canopy. The greater FD-L_{Shoot} based on monoculture than on mixture values (Fig. 2a) and maximum values of mixture-based FD-SLA indicated that efforts to avoid canopy shading through increased height growth are not sufficient and the need to tolerate shading results in a divergence in leaf-level traits. Regarding traits related to nitrogen acquisition and its use (N_{Shoot}, N_{Leaf}, $\delta^{15}N_{Leaf}$), FD did not differ between trait origins in monocultures vs. mixtures. However, FDs were lower (Fig. 2g–i) and CWMs considerably higher (Fig. 1g–i) when trait data from solitary plants instead of monocultures or mixtures were used in the calculations. Probably, access to nitrogen was strongly regulated by neighboring plants. While the increase in FD-N_{Shoot} and FD-N_{Leaf} with increased sown species richness did not depend on trait origin, the increase in FD-$\delta^{15}N_{Leaf}$ was most pronounced with the community-specific trait origin (Appendix S1: Table S3). This supported earlier results that species shift their uptake patterns of N or legumes provide a larger proportion of symbiotically fixed N_2 in more diverse plant communities, and thereby increase complementarity (Gubsch et al. 2011*b*, Roscher et al. 2011*b*).

Trait-based predictions of biomass production and biodiversity effects

Interspecific trait differences have been identified as key factor explaining positive biodiversity–productivity relationships in several experimental studies (Flynn et al. 2011, Roscher et al. 2012, Siebenkäs et al. 2016). In these studies, the role of intraspecific trait variation in response to increasing plant diversity was ignored. Intraspecific trait variation may affect trait-based predictions of community performance and the identification of underlying mechanisms in two ways, which we considered in our study: first, goodness of fit of model predictions may depend on the origin context of trait data, i.e., the growth conditions under which traits are measured. Second, it is possible that predictor variables included in the best models vary dependent on trait origin. We are aware of only a single study considering the effects of trait plasticity in response to biotic interactions in predicting community-level light capture in grassland ecosystems from traits: using a simple wheat-maize intercropping system, Zhu et al. (2015) showed that the predicted performance of the mixed species system deviated strongly from the observed performance when modeling was based on monoculture traits. Our analyses, based on a more complex system, also clearly showed that the origin of trait data matters when trait-based approaches are used to predict processes at the community level.

Indices based on traits of solitary plants were the weakest predictors for community biomass production (Table 3). The model best explaining community biomass production was a model based on CWMs with mean mixture traits, but models with monoculture or community-specific trait data achieved a similar goodness of fit (Fig. 3a). These models clearly showed that community means in traits related to spatial expansion (i.e., large CWM-L_{Shoot}, CWM-MHR, CWM-C_{Shoot}) and the acquisition of nitrogen (i.e., large CWM-N_{Shoot}) were important for high community biomass production. In addition, low CWM-$\delta^{15}N_{Leaf}$ was incorporated in the models, suggesting that high proportions of N_2-fixing legumes (leading to $\delta^{15}N_{Leaf}$ values close to zero) or shifts in the uptake of different N forms (Gubsch et al. 2011*b*) were related to high community biomass. In contrast, the identity of the incorporated FD-based predictors varied more between the different trait origins (Table 3) and led to a more variable goodness of fit (Fig. 3a, b). Obviously, the "functional" adjustments of species in a population or community context affecting both CWMs and FDs were important for community performance.

Community-specific traits only slightly improved model predictions for complementarity and selection effects compared to models based on monoculture or mean-mixture traits. In general, models with both CWMs and FDs best explained complementarity and selection effects, as already shown in Roscher et al. (2012). Irrespective of trait origin in monocultures or mixtures, high CWM-MHR and CWM-N_{Shoot} were related to larger complementarity effects, suggesting that a more complete occupation of canopy space and high levels of nitrogen acquisition are important for large complementarity effects. The CWM part of the best model based on traits of solitary plants deviated strongly from models based on traits measured in monocultures or mixtures with respect to the chosen traits, emphasizing that variation in trait expression as response to neighboring plants changes the "functioning" of species. Differences in traits chosen in the FD parts of the models based on different trait datasets were even stronger, which is not surprising considering the lower correlations among FD based on different trait datasets (Appendix S1: Fig. S5). Specifically, low FD-L_{Shoot} and high FD-N_{Shoot} were incorporated in models based on community-specific traits, suggesting that complementarity effects are greatest when height differences among species are reduced and differences in nitrogen acquisition strategies are increased through plastic responses. A weak consistency in traits chosen in the best models based on different trait origins was also evident in analyses of selection effects. Analyses of selection effects (SE) based on community-specific traits showed that SEs were particularly large when tall-growing species were combined with species limited in height growth (high FD-L_{Shoot}), which varied in photosynthetic capacity (high FD-$\delta^{13}C_{Leaf}$). Interestingly, the FD model best explaining net biodiversity effects was based on monoculture traits. One possible explanation is that species biomass in monoculture enters the calculation of biodiversity effects with the additive partitioning method (Loreau and Hector 2001) and that monoculture traits were closest related to between-species differences in monoculture performance.

Our additional analyses using predictor variable combinations of the best model with CWM and FD based on community-specific traits in models with traits of different origin showed that coefficients of determination in models with traits of different origin were lower than with the community-specific traits (Fig. 3 b, d, f, h). Under the

assumption that community-specific trait values are more appropriate than traits of other origins for choosing the best predictor variable combination these results confirm that values of other origin are not as good as the community-specific traits. However, for community biomass, complementarity and net biodiversity effects, differences between models with monoculture, mean-mixture or community-specific trait origin were again small. In contrast, models with traits of solitary plants were more different. These results provided additional evidence for the "functional" adjustment of plants growing with neighbors.

It is important to mention that the CWM and especially FD of different traits were often correlated (Appendix S1: Table S8). Although FDs for all single traits increased with increasing species richness (except for FD-MHR), we found more variable effects of plant diversity on CWMs. These trait-specific responses of FDs and CWMs to increasing plant diversity support the view that multivariate trait-based indices may complicate the interpretation of underlying patterns, especially if patterns are associated with different niche axes (Butterfield and Suding 2013).

Conclusions

Our results suggest that quantifying the role of interspecific differences and intraspecific trait variation in response to varying biotic interactions will help us better understand the mechanisms underlying biodiversity–ecosystem functioning relationships. Our analyses clearly show that the context in which traits are measured, both in terms of environmental and biotic characteristics, is important for trait-based analysis of ecosystem processes. First, the origin of trait data affects the predictability of ecosystem processes, although further studies are required to better understand that not always traits studied in the community context best predict community performance. Second, the origin of trait data may modify the identity of traits identified as most important for these processes. This observation thus calls for caution and more knowledge about trait origin when using trait-based approaches for community modeling.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2216/suppinfo

Data Availability

Data related to this manuscript are available on PANGEA at https://doi.org/10.1594/pangaea.846582 and https://doi.org/10.1594/PANGAEA.866315.